

Dental Microwear and Microstructure in Early Oligocene Primates From the Fayum, Egypt: Implications for Diet

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ABSTRACT Textbook descriptions usually portray the Fayum anthropoids as frugivores, with *Parapithecus grangeri* including a folivorous component in its diet and *Apidium* a component of hard-object feeding. Recent work with modern mammals has shown that analyses of both dental microwear and dental microstructure may yield insights into diet and tooth use. The purpose of this study was to combine these two techniques to gain a better perspective on the paleobiology of the Fayum higher primates.

Dental microwear analyses involved the use of high resolution epoxy casts of *Aegyptopithecus*, *Parapithecus*, and *Apidium* housed in the Duke University Primate Center. Scanning electron micrographs were taken at $\times 500$, and all microwear features in each micrograph were digitized. For microstructure analyses, molar teeth were sectioned in a variety of planes, lightly etched, and photographed in the SEM.

Results of the dental microwear analyses indicate that the three Fayum anthropoids all clustered with modern primate frugivores but that there were also significant differences between *Aegyptopithecus* and the other two Fayum genera. By contrast, dental microstructure analyses showed important differences between *Apidium* and the other two genera. The reason for these differences probably lies in a combination of body size and dietary differences, with *Aegyptopithecus* occasionally feeding on hard objects and *Apidium* maximizing wear resistance through a unique emphasis of radial (rather than decussating) enamel. © 1996 Wiley-Liss, Inc.

The Jebel Qatrani Formation, in the Fayum Depression of Egypt, has long been known as the world's best source of Oligocene primate material (Bown et al., 1982; Fleagle and Kay, 1987; Kay et al., 1981; Rasmussen and Simons, 1988; Schlosser, 1911; Simons, 1965, 1995). Recent discoveries, and redating of the Eocene-Oligocene boundary, have focused attention on Quarries E and L-41 from the late Eocene portions of this deposit (Rasmussen and Simons, 1992; Simons, 1989, 1990, 1992; Simons and Rasmussen, 1994, 1995; Simons et al., 1994).

However, the abundance of primate material in the upper sequence (formerly known as the "Upper Fossil Wood Zone" [Bown and Kraus, 1988]) leaves a host of paleobiological questions to answer.

In this paper, our interests lie in the diets of the early anthropoids known as *Aegyptopithecus*.

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topithecus zeuxis, *Apidium phiomense*, and *Parapithecus grangeri*. Previous workers (e.g., Fleagle, 1988; Fleagle and Kay, 1985; Kay and Simons, 1980, 1983) have hypothesized that all three species were frugivores. The relatively greater molar shearing capacity of *Parapithecus grangeri* is suggestive of a slightly more folivorous diet (Kay and Simons, 1980), while the thicker molar enamel of *Apidium phiomense* was thought to suggest a diet including harder nuts or seeds (Fleagle and Kay, 1985). However, as compared with other primates, the molars of the Fayum anthropoideans are fairly homogeneous, with low, blunt cusps and relatively little shearing capacity. The purpose of this paper is to use new techniques (dental microwear and microstructure analyses) to reexamine the dietary adaptations of these fossil primates.

MATERIALS AND METHODS

Microwear and microstructure as instruments to measure dental function

Over the past decade, the analysis of microscopic wear patterns on teeth (or dental microwear analysis) has emerged as a valuable method for dietary reconstruction in modern and fossil animals (for recent reviews see Teaford, 1991, 1994; Ungar, 1992a). Its greatest strength lies in the fact that it is ultimately based on a precise, direct record of what an animal *did*, not what that animal was hypothetically, biomechanically, or evolutionarily *capable* of doing. As Teaford (1994:26) recently noted, "[I]t can provide the first 'Polaroid' snapshots of paleobiology—evidence from an evolutionary instant directly from the surface of the fossil." As a result, it can give us new perspectives on many situations—for example, studies of unusual creatures with no modern analogues (Solounias and Hayak, 1993; Solounias et al., 1988), studies of closely related species where traditional studies of tooth shape have yielded equivocal results (Grine, 1986; Teaford, 1993), and intraspecific studies where differences in tooth shape are minimal or nonexistent (Harmon and Rose, 1988; Molleson et al., 1993; Pastor, 1992). While analyses of modern museum material have probably been pushed to their practical lim-

its (e.g., Gordon, 1988; Solounias and Hayak, 1993; Strait, 1993; Teaford and Robinson, 1989; Teaford and Runestad, 1992; Ungar, 1994), ongoing laboratory and fieldwork (e.g., Lucas, 1994; Lucas and Teaford, 1995; Maas, 1991, 1994a; Strait and Overdorff, 1994, 1995; Teaford and Glander, 1991, in press; Teaford and Oyen, 1989a; Ungar, 1992b, 1994; Ungar et al., 1995) is bringing us to a better understanding of the causes of dental microwear. Thus, the time is right to examine the dental microwear of the Fayum anthropoideans—to see how the evidence of tooth use compares with that of tooth shape.

Also, understanding of the functional importance of dental microstructure has increased tremendously in recent years. The newer studies have reemphasized that dental enamel is an incredibly complicated structure (e.g., Koenigswald and Clemens, 1992), and the functional implications of variations in microstructure are likewise complex (e.g., Boyde and Fortelius, 1986; Fortelius, 1985; Koenigswald et al., 1987; Maas, 1991, 1993, 1994a,b; Rensberger, 1993; Rensberger and Koenigswald, 1980). On a scale of increasing complexity, enamel consists of three levels of structure: 1) crystallites (the smallest structural units), 2) prisms (bundles of crystallites), and 3) enamel types (groups of prisms). These different levels of enamel complexity influence different aspects of dental function. Thus, differences in orientation of enamel crystallites relative to occlusal surfaces of teeth may affect the resistance of a tooth to abrasion (small-scale tissue loss), whereas differences in enamel types pertain to resistance to fracture and consequent large-scale tissue loss.

While investigators have long suspected that variations in enamel microstructure might have a significant influence on dental microwear patterns (Boyde and Fortelius, 1986; Boyde and Martin, 1982, 1984; Martin et al., 1988; Puech, 1984; Rensberger, 1978), many of those suspicions were posed almost as either-or alternatives: either the observed patterns were caused by food or they were caused by microstructure. Work by Maas (1991, 1993, 1994a) has shown that dental microstructure and dental function are in-

terdependent. However, this relationship is not an either-or proposition; sometimes dental microstructure can influence dental microwear (e.g., the width of scratches produced by certain movements), and other times it apparently cannot (e.g., the size of pits produced by different sized abrasive particles). Because of this, interspecific comparisons of crystallite orientations, for example, can strengthen interspecific comparisons of diet based on microwear patterns. Likewise, at another structural level, documentation of interspecific variation in enamel types may strengthen arguments for fundamental mechanical differences between teeth of difference species.

In light of the above, it is safe to say that both dental microwear and dental microstructural analyses can yield significant insights into dental function. The question we wish to ask is what they can tell us about dental function and diet in the Fayum anthropoideans.

Microwear

All the Fayum primates were studied at the Duke Primate Center (DPC) where they were initially examined under a dissecting microscope at 20 \times magnification. Specimens that showed no enamel or sufficient postmortem wear to preclude microwear analysis were not used in this portion of the study¹. Remaining specimens were gently swabbed with acetone to remove dirt, dust, or grease and allowed to sit overnight. Polysiloxane impressions were then taken of M2 using Coltene's President Jet Regular impression material (Beynon, 1987; Rose, 1983; Teaford and Oyen, 1989b). As in previous microwear studies (e.g., Teaford, 1991, 1993, 1994; Teaford and Robinson, 1989; Teaford and Runestad, 1992), epoxy casts were made from the resultant molds and used in scanning electron microscopy. Micrographs of the crushing facets of upper or lower M2 were taken at a magnification of 500 \times on an AMRAY 1810 scanning electron microscope (SEM) in

secondary emissions mode (see Table 1 for a list of specimens used).² All micrographs were digitized as described in the aforementioned studies. Average computed measurements (for each specimen) included the following: number of features per micrograph, percentage of pits, pit width, and scratch width. All data for each species were tested for normality and homogeneity of variances using the Kolmogorov-Smirnov test with Lilliefors's correction and Bartlett's test for homogeneity of variances, respectively (Zar, 1984). To meet these underlying assumptions of parametric statistical analyses, measures of pit width and the number of features per field were log-transformed, measures of the percentage of pits were arcsine-transformed, and measures of scratch width were rank-transformed before analysis.³ Statistical comparisons involved single factor ANOVA followed by Tukey's HSD test (Zar, 1984).

Microstructure

Isolated molars of *Aegyptopithecus zeuxis*, *Parapithecus grangeri*, and *Apidium phiomense* were prepared for documentation of the following aspects of enamel microstructure: 1) crystallite and prism orientations and enamel types (longitudinal sections), 2) prism packing patterns (surface-tangential sections), and 3) occlusal surface microstructure (natural occlusal surfaces). Sample sizes consisted of one or two upper or lower molars per species (Table 1); studies of variation in living primates demonstrate that this is adequate for documenting the aspects of interspecific variation in enamel microstructure we consider here (Maas, 1993, 1994b).

Methods of specimen preparation are described in detail elsewhere (Maas, 1993, 1994b; Maas and Thewissen, 1995) and can be briefly summarized as follows. For preparation of longitudinal and surface-tangential sections, the molars were embedded in epoxy

¹Postmortem wear is generally surprisingly easy to recognize because the occlusal and nonocclusal surfaces of the tooth usually show distinctive wear patterns (Grine, 1977, 1986; Teaford 1988b). The interproximal facets are particularly useful in this regard.

²Given the vagaries of fossil preservation, any of the phase II crushing facets recognized by Kay (1977) (i.e., facets 9, 10n, or x) were used in this study.

³Previous work by Conover and Iman (1976) has shown that transformations can sometimes meet the underlying assumptions of parametric tests and thus yield more robust analyses than nonparametric techniques.

TABLE 1. List of fossil specimens used in this study

Species used for microwear analysis		Duke Primate Center (DPC) specimen number	
<i>Aegyptopithecus zeuxis</i>		1027, 3056, 3144, 3837, 5391, 6100, 7258	
<i>Parapithecus grangeri</i>		2376, 2385, 6313, 8793, 8796	
<i>Apidium phiomense</i>		1037, 1048, 1119, 1124, 2412, 2943, 3080, 3133, 3827, 3881, 3906, 3909, 5273, 5389, 6137, 6253B, 7249, 7857, 11168, 11171, 11423	
Species used for microstructure analysis	Specimen	Tooth	Preparation
<i>Apidium phiomense</i>	DPC 1940A	Lmx	Longitudinal section Surface-tangential section
	DPC 1940B	Rmx	Longitudinal section
	DPC 1940D	Lmx	Occlusal surface
	DPC 1013B	Lm2	Longitudinal section Surface-tangential section
<i>Parapithecus grangeri</i>	DPC 1013F	Rm2	Longitudinal section
	DPC 1013H	Rm1	Occlusal surface
	DPC 5855	RM3	Longitudinal section Surface-tangential section
<i>Aegyptopithecus zeuxis</i>	DPC 2298	Lm2	Occlusal surface Longitudinal section

resin and sectioned buccolingually in a plane perpendicular to the occlusal plane (longitudinal sections). On the buccal surface of one-half of each sectioned tooth, a facet was ground tangential to the outer surface (surface-tangential sections). Because prism pattern varies with depth from surface in many species (e.g., Grine et al., 1987; Maas, 1993, 1994b), these surface-tangential sections were prepared perpendicular to the cut face of longitudinal sections to ensure that similar depths of enamel were examined for each specimen. Sectioned specimens were polished (800 and 1200 silicon carbide paper and 0.05 μm alumina oxide powder) and lightly etched (2.5% HCl for 10 sec). In addition, in order to document microstructure at naturally worn occlusal surfaces, whole teeth or longitudinally sectioned specimens were mounted crown upwards on SEM stubs and lightly etched. All specimens were coated with gold palladium and examined in a JEOL 35-C SEM in secondary emissions mode. To document prism patterns, micrographs of surface-tangential sections were taken at $\times 2,000$. To illustrate enamel types and crystallite orientation, micrographs of longitudinally sectioned teeth were taken at $\times 200$ – $\times 2,000$. For study of crystallite orientation, at functionally distinct naturally worn molar occlusal surfaces, cusp tip facets and chewing wear facets were photographed at $\times 2,000$.

RESULTS

Microwear

Of the available specimens at the Duke Primate Center, 60–70% (depending on the species in question) could not be used due to postmortem wear. Most of those specimens were identified and excluded from the analysis based upon examination with a light microscope. For example, out of 70 specimens of *Apidium*, 37 (53%) were excluded based on light microscope examination at the DPC. Ten specimens (14%) showed more subtle postmortem wear which could only be identified in the SEM. Specimens of *Propithecus chirobates* were also examined at the DPC, but all had too much postmortem wear to be used in the microwear portion of this project.

There were two significant differences in dental microwear between the Fayum species. *Aegyptopithecus* showed significantly less microwear ($P < 0.009$) and significantly wider pits ($P < 0.02$) than did *Apidium phiomense* (see Table 2; Figs. 1, 2). Differences in the amount of dental microwear between *Aegyptopithecus* and *Parapithecus* approached significance ($P < 0.067$).

Microstructure

The different levels of enamel structure (crystallites, prisms, enamel types) showed different patterns of variation. At the small-

TABLE 2. Summary of molar microwear data

Species	Number of features per micrograph (\pm s.d.)	% Pits (\pm s.d.)	Average pit width (\pm s.d.)	Average scratch width (\pm s.d.)
<i>Aegyptopithecus</i> (N = 7)	107 (\pm 29)	31.8 (\pm 9)	5.5 (\pm 2.5)	1.2 (\pm 0.3)
<i>Parapithecus</i> (N = 5)	152 (\pm 24)	28.2 (\pm 13)	3.6 (\pm 1.1)	1.0 (\pm 0.05)
<i>Apidium</i> (N = 22)	166 (\pm 48)	34.3 (\pm 7)	3.6 (\pm 0.8)	1.0 (\pm 0.12)

est structural level, that of the crystallite, interspecific variation was minimal. In all cases crystallites in prismatic and interprismatic enamel formed angles of less than 45° to one another (Fig. 3).

In both *Aegyptopithecus* and *Parapithecus*, there were differences in the orientations of crystallites relative to the occlusal surfaces between cusp tip facets and chewing wear facets. In these species, the cusp tips (which are important in puncture-crushing) were characterized by a large proportion of surface-parallel crystallites (mostly interprismatic crystallites), whereas both prismatic and interprismatic crystallites on chewing wear facets (which are formed by close contact as teeth slide past one another during chewing) intercepted the surface at angles slightly oblique to normal (Fig. 4C–F). By contrast, in *Apidium*, both cusp tip facets and chewing wear facets were characterized by crystallites oriented normally to or slightly obliquely to the surface (Fig. 4A, B). It is important, however, that orientations of crystallites relative to chewing wear facet surfaces were similar for all three species. This suggests that interspecific comparisons of microwear on chewing wear facets would not be influenced by differences in microstructure.

At the next structural level, that of the prism (illustrated by prism patterns), there was no apparent interspecific variation. *Aegyptopithecus*, *Parapithecus*, and *Apidium* all showed a predominance of pattern 3 prisms (arc-shaped prism boundaries, with prisms arranged in horizontally offset rows) (Fig. 5). As with most fossil and Recent primates examined to date (e.g., Boyde and Martin, 1987; Martin et al., 1988; Maas, 1993, 1994b), there was considerable individual variation in prism shape and size. Pattern 1 prisms (closed, circular prism boundaries) also occurred in each species but

were largely confined to the outer (superficial) enamel, as is typical of many primates (e.g., Boyde and Martin, 1987; Martin et al., 1988; Maas, 1993, 1994b; Maas and O'Leary, in press).

At the structural level of the enamel type there was more interspecific variation than at the crystallite or prism levels. All species showed a very thin layer of nonprismatic enamel close to the surface (again, as is typical of many primates), but the deeper enamel differed among taxa. *Parapithecus* and *Aegyptopithecus* showed a thin outer layer of radial enamel (prisms with long axes parallel to one another) underlain by a much thicker layer of decussating enamel (groups or zones of prisms with long axes parallel to one another but at an angle to long axes of prisms in adjacent decussation zones) (Fig. 6B,C). In sharp contrast, the very thick enamel cap of *Apidium phiomense* consisted almost entirely of radial enamel, with no trace of prism decussation (Fig. 6A).

DISCUSSION

Microwear

The amount of postmortem wear on the Fayum primate teeth is probably to be expected, given that most specimens were probably deposited after being washed some distance in sandy streams and later exposed at the surface to abrasion by wind-blown sands (Simons, 1967). From that perspective, it is perhaps surprising that so many specimens were usable in the dental microwear analyses. It is also encouraging that light microscope examination was generally successful in identifying specimens with postmortem wear, as this might save effort and expense in future museum work. The amount of postmortem wear of Fayum fossils is similar to that encountered in monkey and ape material at Koobi Fora and Rusinga in

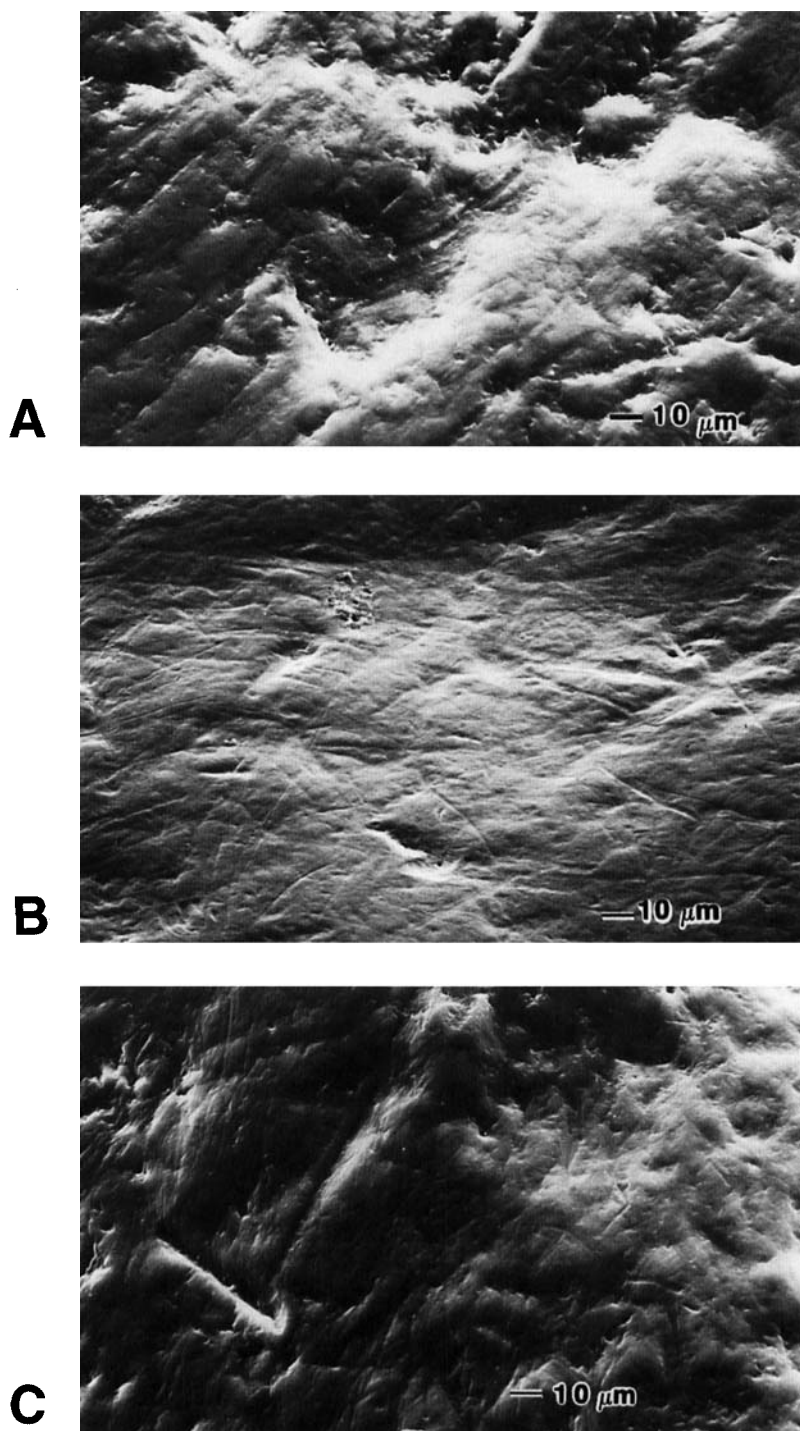


Fig. 1. SEM micrographs of crushing areas on M2 of Fayum anthropoids. **A:** *Aegyptopithecus zeuxis*. **B:** *Parapithecus grangeri*. **C:** *Apidium phiomense*.

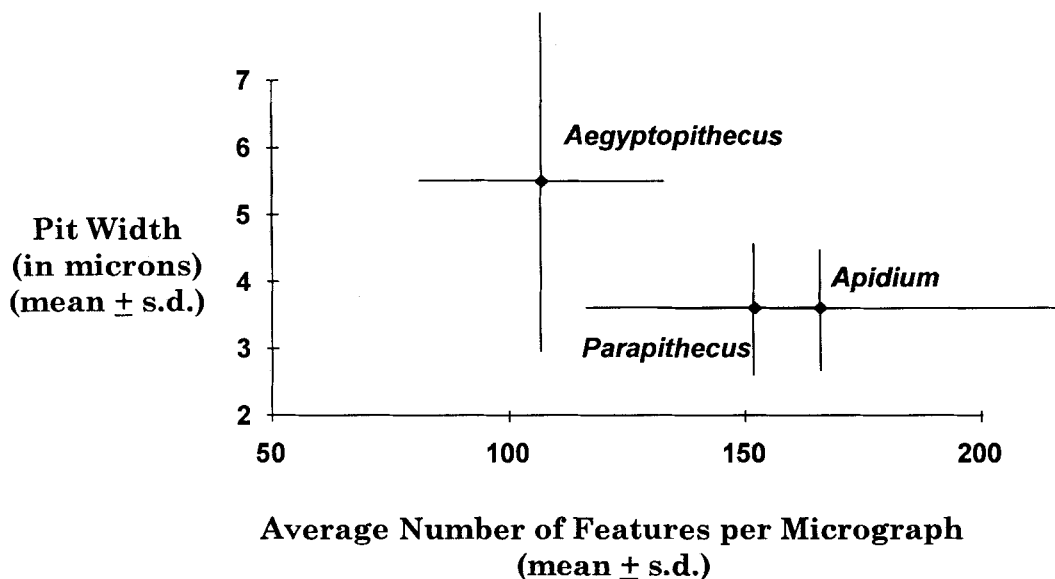


Fig. 2. Bivariate plots of molar microwear measurements for crushing areas on M2 of Fayum anthropoids.

Kenya but greater than that encountered at West Turkana and Songhor in Kenya (Teaford and Leakey, 1992).

By itself, the microwear data tells us a number of things about the Fayum anthropoids. Judging from the incidence of pitting on the teeth, *Aegyptopithecus*, *Apidium*, and *Parapithecus* were all essentially frugivorous (see Fig. 7). To statistically test this hypothesis, a single factor ANOVA was run using previously published data for extant anthropoids (Rafferty and Teaford, 1992; Teaford, 1988a, 1993; Teaford and Runestad, 1992). The extant species were placed in three diet groups based on published information: folivores, mixed feeders (mainly frugivores), and hard-object feeders (see Table 3). To meet the assumptions of parametric statistical analyses, data were rank-transformed before analysis. All three Fayum primates showed significantly more pitting on their molars than did the modern primate folivores (see Fig. 7). Thus, if *Parapithecus* had a folivorous component to its diet (as suggested by studies of molar shearing capacity [Kay and Simons, 1980]), it was

unlike most modern primate folivores.⁴ If we had to pick an analogue from among modern primate folivores, it would be a more frugivorous "folivore" such as *Alouatta palliata* from seasonal, dry forest sites in Costa Rica (Teaford and Glander, 1991, in press). As only five specimens of *Parapithecus* proved useful for microwear analysis, the higher incidence of pitting on their teeth might also be an artifact of small sample size. However, the molar microwear similarity with modern primates from seasonal environments is also intriguing in light of previous suggestions of seasonal variations in rainfall in the Oligocene Fayum forest (Bown et al., 1982).

It should also be noted that, in the aforementioned single factor ANOVA, *Apidium* and *Aegyptopithecus* showed significantly more pitting than did the modern primate mixed feeders, and none of the Fayum primates could be distinguished from the mod-

⁴As *Parapithecus* had less molar shearing capacity than in modern hominoid folivores (Kay and Simons, 1980), this is perhaps not surprising.

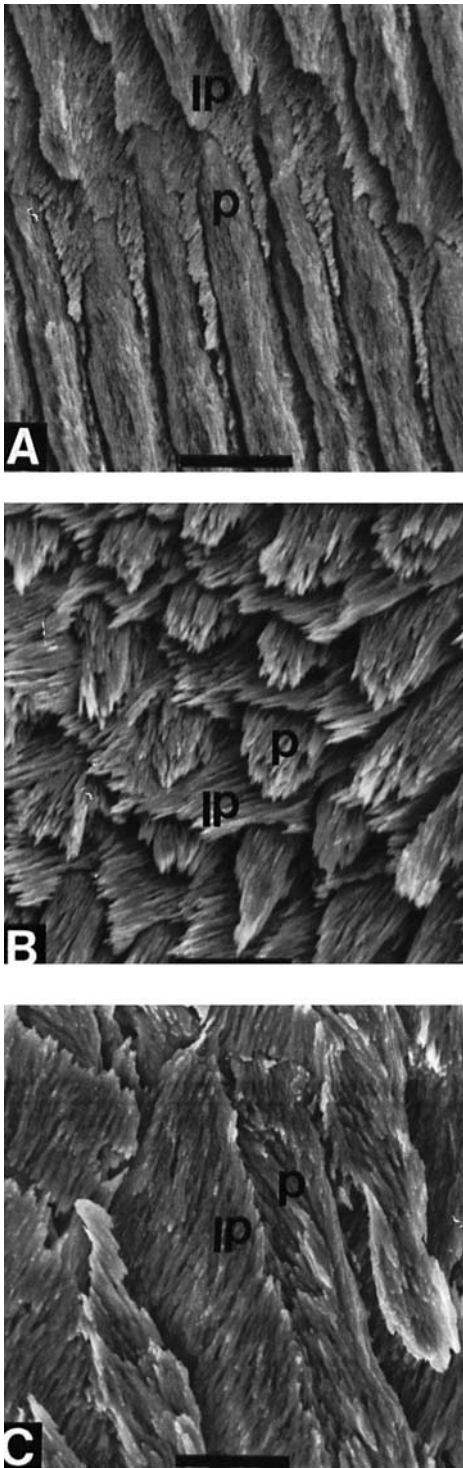


Fig. 3. High magnification micrographs of longitudinally sectioned molars illustrating relative orientation of prismatic (P) and interprismatic (IP) crystallites. **A:** *Apidium phiomense*. **B:** *Parapithecus grangeri*. **C:** *Aegyptopithecus zeuxis*. Scale bars, 100 μm .

ern hard-object feeders based on the incidence of pitting on their molars (although *Parapithecus* approached significance with $P < .087$). When a similar analysis was run for pit width, however, both *Apidium* and *Parapithecus* showed significantly narrower pits than did either the modern primate mixed feeders or the hard-object feeders. Based on the incidence and size of the pitting on its molars, *Aegyptopithecus* seems more closely allied with modern primate hard-object feeders, although, again, this should be tested with larger samples of *Aegyptopithecus*.

The differences in molar microwear between *Aegyptopithecus* and *Apidium* would seem to yield some additional insights into the paleobiology of these early anthropoids. The amount of microwear on the teeth of *Apidium* suggests that it had a more abrasive diet than did *Aegyptopithecus*. However, its relatively small average pit size would seem to indicate that *Apidium* was not a hard-object feeder. *Aegyptopithecus*, by contrast, might have been, but maybe not in the same sense as some of the classic modern hard-object feeders like *Cercocebus albigena*. The only clue as to the difference between the two fossil species lies in the large range of pit widths shown by *Aegyptopithecus*. Despite its small sample size, *Aegyptopithecus* shows a much larger range of pit widths than do either of the other Fayum anthropoids (see Fig. 8)—a range which is larger than that of most of the modern hard-object feeders examined to date. This raises the possibility that *Aegyptopithecus* might have had a more variable diet than did *Apidium*, *Parapithecus*, or the various modern primate hard-object feeders for that matter. Could it be that *Aegyptopithecus* included hard objects in its diet only in response to seasonal changes in resource availability? It is a distinct possibility, but far more work (on larger samples and other teeth) is needed before we can feel more certain of this possibility. However, because pit size has been shown to vary with size of abrasive particles (Maas, 1994a), at the very least, we can conclude with confidence that there were some significant differences in the feeding habits of *Aegyptopithecus* and *Apidium* and that these differences reflect the different sizes and

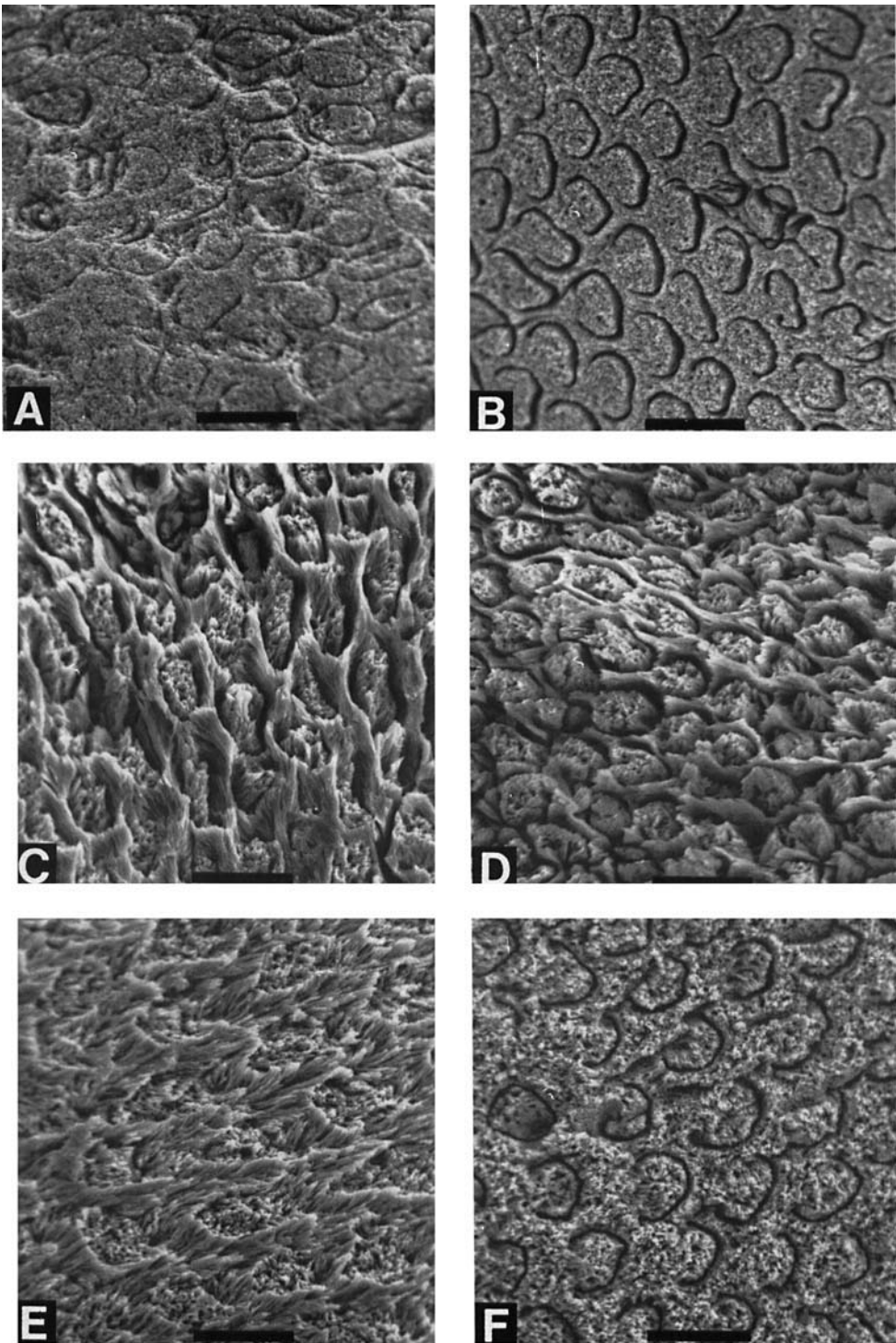


Fig. 4. High magnification micrographs of occlusal surfaces, illustrating orientation of crystallites relative to naturally worn surfaces. **A:** *Apidium phiomense*, tip hypoconid. **B:** *Apidium phiomense*, wear facet 3. **C:** *Parapithecus grangeri*, tip metaconid. **D:** *Parapithecus grangeri*, wear facet 6. **E:** *Aegyptopithecus zeuxis*, tip protocone. **F:** *Aegyptopithecus zeuxis*, wear facet 9. Scale bars, 100 μm .

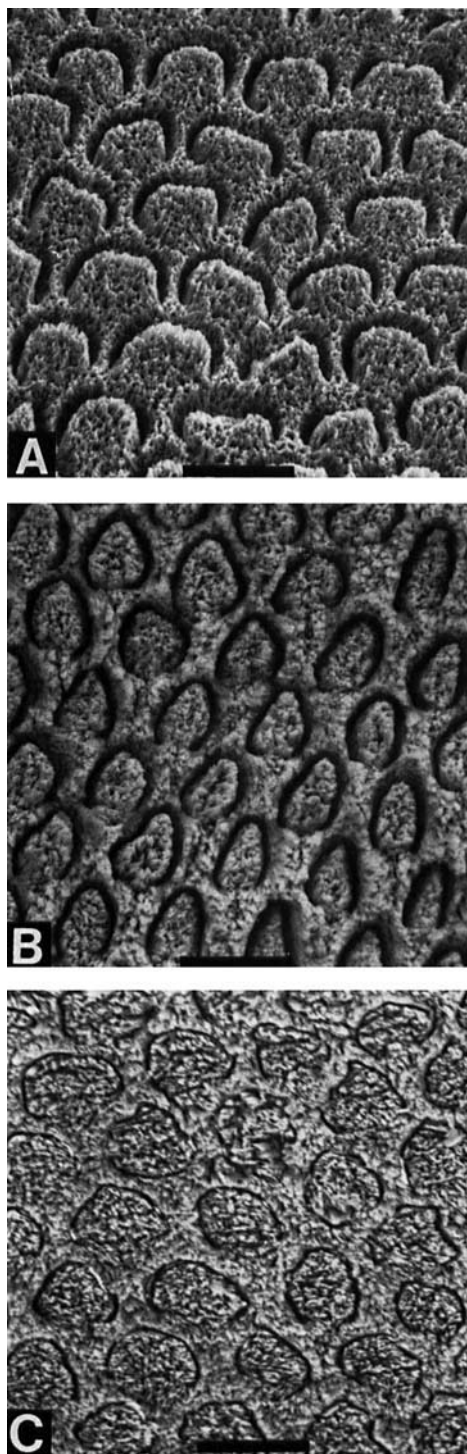


Fig. 5. High magnification micrographs of surface-tangential facets, illustrating prism packing patterns. **A:** *Apidium phiomense*. **B:** *Parapithecus grangeri*. **C:** *Aegyptopithecus zeuxis*. Scale bars, 100 μm .

quantities of abrasive particles ingested along with their food. We also cannot reject the possibility that *Aegyptopithecus* occasionally fed on, or ingested, hard objects.

Microstructure

At the structural levels of the crystallite and prism, the Fayum anthropoideans differ little from other early Tertiary primates examined to date. Predominance of pattern 3 prisms is characteristic of the late Eocene Fayum higher primates *Catopithecus browni* and *Apidium moustafai* (Maas and Simons, 1995) as well as the early Eocene notharctines *Cantius* and *Notharctus* (Maas and O'Leary, in press). These aspects of their microstructure also are similar to the largely frugivorous lemurid primates (Maas, 1994b) and may well be primitive for the order. Nevertheless, by looking at the mechanical properties conferred by these and other microstructural features, we can gain further insights into dental function and thus the paleobiology of the Fayum anthropoideans.

The differences in crystallite orientations between cusp tip facets and chewing wear facet surfaces seen in *Parapithecus* and *Aegyptopithecus* are similar to those seen in the extant strepsirrhine primates *Otolemur crassicaudatus*, *Lemur catta*, and *Eulemur* spp. Maas (1993) argued that predominance of surface-parallel crystallites at cusp tips and of surface-oblique crystallites at chewing wear facets optimizes resistance to abrasive wear in both regions. This interpretation assumes that the largest component of masticatory force is normal to the occlusal surface at cusp tips (as expected during puncture-crushing of food items) and is parallel to the occlusal surface at chewing wear facets (as upper and lower teeth slide past one another during chewing). Given this, the more uniform occlusal orientation of crystallites in *Apidium*, where all crystallites are more or less oblique to the tooth surface, is intriguing. Was there some fundamental difference in the way that *Apidium* chewed (was puncture-crushing less important?), or did *Apidium* molars maintain their durability in some other fashion? The molars of *Apidium* are also more polycuspidate than are those of any other Fayum primate.

One diagnostic attribute of *Apidium* molars is their very thick enamel cap. Based

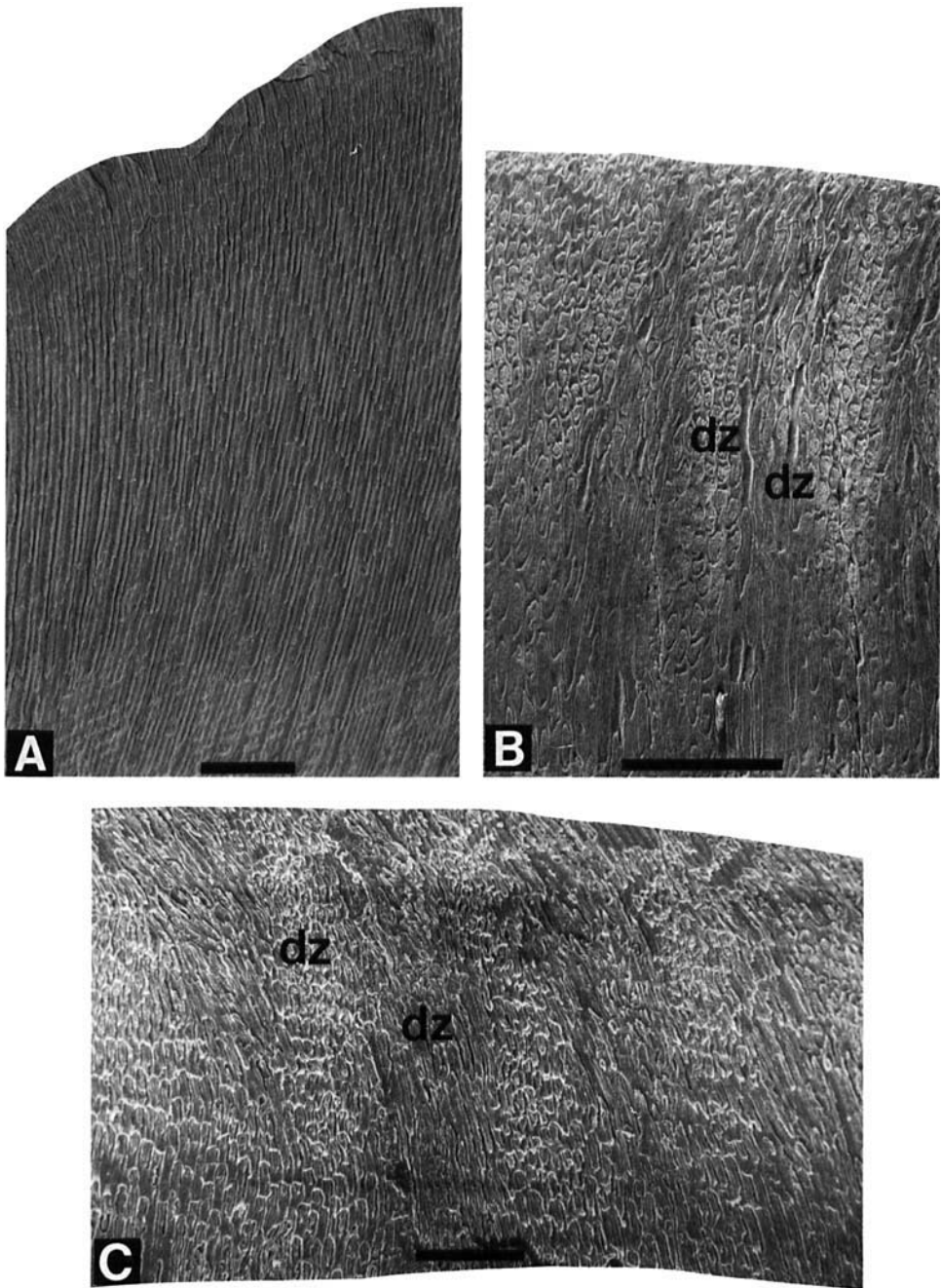


Fig. 6. Micrographs of longitudinally sectioned molars illustrating enamel types. Sections are oriented with enamel-dentine junction at bottom. Prisms in adjacent decussation zones (dz) differ in orientation. **A:** *Apidium phiomense*. **B:** *Parapithecus grangeri*. **C:** *Aegyptopithecus zeuxis*. Scale bars, 100 μm .

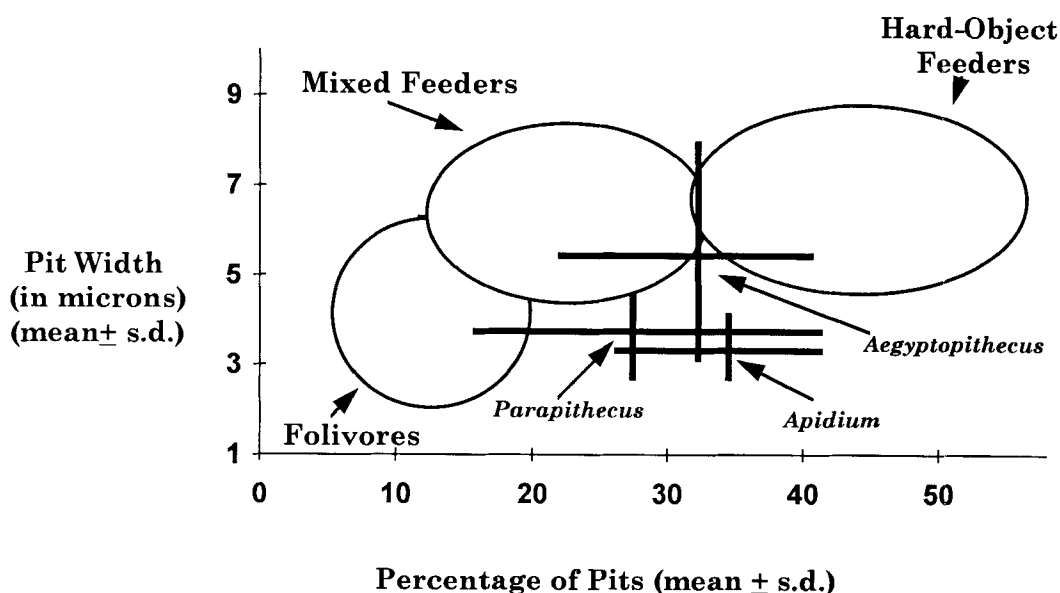


Fig. 7. Bivariate plot of molar microwear in the Fayum anthropoids vs. modern primate folivores, mixed feeders/frugivores, and hard-object feeders. Ellipses for modern primates represent means \pm one standard deviation for each diet group. Cross hairs for Fayum anthropoids also represent means \pm one standard deviation.

TABLE 3. Extant specimens used in statistical comparison with Fayum anthropoids (N)

Folivores: <i>Colobus guereza</i> (10), <i>Procolobus badius</i> (10), <i>Gorilla gorilla</i> (10), <i>Presbytis entellus</i> (9), <i>Alouatta seniculus</i> (6), <i>Alouatta palliata</i> (from Panama) (14), and <i>Theropithecus gelada</i> (17)
Mixed feeders/frugivores: <i>Pan troglodytes</i> (10), <i>Papio cynocephalus</i> (12), <i>Cebus capucinus</i> (10), <i>Cebus nigrivittatus</i> (62), <i>Cebus albifrons</i> (2), <i>Ateles belzebuth</i> (11), <i>Saimiri sciureus</i> (13), and <i>Aotus trivirgatus</i> (11)
Hard-object feeders: <i>Cercocebus albigena</i> (10), <i>Cebus apella</i> (10), <i>Pongo pygmaeus</i> (10), <i>Pithecia pithecia</i> (11), <i>Chiropotes satanas</i> (18)

on the sectioned molars used in this study, *Apidium* has an enamel thickness index (Martin, 1985) greater than any other Fayum anthropoid; indeed, its enamel thickness index is more than twice that of *Aegyptopithecus* (Table 4). In primates, such thick enamel is generally associated with hard-object feeding (Kay, 1981). However, extant primate hard-object feeders invariably show strong prism decussation, a feature linked to enamel fracture resistance (Pfretzschner, 1986), and *Apidium* shows no vestige of prism decussation. Here it also is worthwhile to recall the absence of surface-paral-

lel crystallites (presumably resistant to abrasion by predominantly surface-normal forces) at *Apidium*'s molar cusp tips, where high surface-normal forces might be expected in an animal that uses its cheek teeth to fracture hard objects.

It should be emphasized that although both *Aegyptopithecus* and *Parapithecus* do show prism decussation, this does not necessarily imply that these animals were adapted to hard-object feeding. Although those living primates sampled to date that regularly masticate hard objects always have decussating enamel, some primates that typically feed on softer food items also show prism decussation (e.g., *Alouatta palliata*, *Lemur catta*, *Eulemur* spp.). Comparative studies of a broad taxonomic sample of mammals suggest that the constraining factor is body size: herbivorous mammals with molar widths greater than 4 mm almost invariably show prism decussation, whereas smaller herbivores rarely do (Koenigswald et al., 1987). According to this hypothesis, prism decussation is an adaptation to increased chewing stresses associated with in-

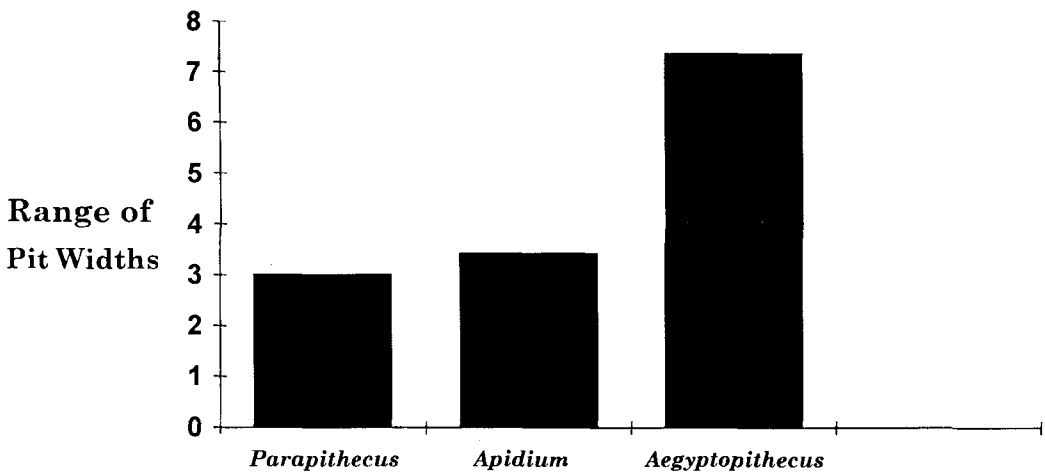


Fig. 8. Range of pits widths on M2s of Fayum anthropoids.

TABLE 4. Enamel thickness indices for Fayum anthropoids¹

Species	Enamel thickness index
<i>Apidium moustafai</i>	23.55
<i>Apidium phiomense</i>	25.33
<i>Parapithecus grangeri</i>	15.05
<i>Aegyptopithecus zeuxis</i>	9.98
<i>Propliopithecus chirobates</i>	18.37

¹Index is calculated as $(c/e \times 100)/b^{1/2} \times 100$, where c is the area of the enamel cap, e is the length of enamel-dentine junction, and b is the combined area of the dentine and pulp cavity contained within the enamel cap (Martin, 1985). N = 1 for each species.

creased body size and not a special adaptation for hard-object feeding per se. There are some exceptions to this "rule." Prism decussation does occur in smaller species, including many rodents (Koenigswald et al., 1987), some early ungulates (Maas and Thewissen, 1995), and some callitrichine primates (Propst, 1995). However, the pattern of distribution of enamel types that we see in the Fayum anthropoids is consistent with the body size constraint explanation. The largest taxa (*Aegyptopithecus* and *Parapithecus*) show prism decussation, whereas the smaller *Apidium phiomense* does not. The enamel structure of the other Fayum anthropoids, including the relatively large *Propliopithecus chirobates* (prism decussation present) and the small *Apidium moustafai* and *Catopithecus browni* (prism decussation absent) also fits the size constraint pattern (Maas and Simons, 1995).

Combined microwear and microstructure analyses

The results of the combined analyses for *Aegyptopithecus* and *Parapithecus* are complementary but not surprising and are largely consistent with previous interpretations based on gross morphology. Both species show similar microstructure, and both were probably frugivores, with *Aegyptopithecus* occasionally ingesting hard objects and *Parapithecus* having a variable yet abrasive diet. The combination of dental microwear and dental microstructure analysis, however, sheds considerable new light on the interpretation of the dietary habits of *Apidium*. Morphologically, *Apidium* is unique among primates in its combination of thick enamel and radial prisms. Both the microstructural data (lack of microstructural mechanisms to resist large-scale fracture) and the microwear data are inconsistent with the idea that *Apidium* was a hard-object feeder. *Apidium* does, however, show a high incidence of microwear, characteristic of living primates with very abrasive diets.

Highly abrasive diets present a different mechanical challenge to tooth durability than do hard objects. The challenge is resistance to small-scale tissue loss rather than resistance to large-scale tissue loss caused by catastrophic fractures. One strategy to enhance tooth durability in a highly abrasive

regime would be to change the orientation of crystallites relative to wear surfaces; if we assume a large surface-parallel component of chewing force, this orientation optimally would be perpendicular or slightly oblique to the wear surface (Maas, 1993). Another strategy would be to increase the quantity of enamel. *Apidium* molars do both. The orientation of crystallites perpendicular or just slightly oblique to the tooth surface should minimize the amount of tissue lost through abrasive wear caused by opposing surfaces sliding past each other, and the hyperthick enamel cap should ensure a long period of tooth use before the enamel is breached. *Apidium phiomense* may have been close to a threshold in body size above which it would have to develop prism decussation to counter the effects of higher occlusal forces. Based on comparative samples of primates (Maas, 1993, 1994b; Martin et al., 1994) the threshold probably lies somewhere around 1,500–2,000 g. Body size estimates for *Apidium phiomense* have ranged from 1,200–1,700 g (Conroy, 1987), based on dental measurements. It also is possible that *Apidium* had relatively large teeth and thus a smaller body size (e.g., in *Proconsul*) (Walker et al., 1993). Only further analyses of well-documented postcranial material will tell.

Another possible interpretation of the functional significance of the thick enamel of *Apidium* is that it represents an adaptation to protect the tooth from erosion by highly acidic foods. We believe that this is unlikely. First, only some *Apidium* teeth show evidence of etching (prism relief), and prism relief can also be caused by mechanical polishing by soft foods, in any event. Secondly, preliminary studies of primates and bats whose diets regularly include highly acidic or high sugar foods suggest that these animals have thick layers of nonprismatic enamel on their molar teeth (E.R. Dumont, personal communication), and *Apidium* molars, like those of the other Fayum higher primates, have only a very thin outer layer of nonprismatic enamel.

CONCLUSIONS

There are two basic conclusions to be derived from this study. First, we now have a

better idea of the diets of the early Anthropoidea from the Fayum. As has been suggested by analyses of tooth shape, *Aegyptopithecus*, *Parapithecus*, and *Apidium* were probably all frugivores. However, as studies of diets of living primates have shown, “frugivory” subsumes a wide range of dietary habits. With the combination of analyses presented here, we can start to discern some of those additional subtleties. *Aegyptopithecus* probably had the least abrasive diet of the three, although it probably occasionally ate hard objects. Its microwear and tooth shape suggest that it is perhaps most similar to some of the less specialized *Cebus* monkeys such as *Cebus olivaceus*, or perhaps the owl monkey (although the small-bodied owl monkey lacks decussation [Martin et al., 1994]). *Parapithecus* had a fairly abrasive diet and may have been more folivorous than the other two species. If so, its closest modern analogue would probably be one of the more frugivorous “folivores”—such as *Alouatta palliata* from seasonal, dry forest habitats—because these populations show an unusually high incidence of pitting on their molars and spend a significant portion of their time feeding on fruit. *Apidium* is the most intriguing of the three species. Its microwear and microstructure suggest that it had an abrasive diet that probably did not include much in the way of hard objects. Possibly because of its smaller body size, it did not generate high occlusal forces that would require the crack-stopping properties of decussating enamel, but its relatively thick, radial enamel may have been an attempt to resist wear in a highly abrasive dietary regime.

Of course, it is one thing to say that *Aegyptopithecus* and *Apidium* ingested different amounts or types of abrasives; it is quite another to say why that was so. Unfortunately, at the present time, we cannot identify those abrasive particles with certainty. Many primate foods are so soft that they do not leave distinctive dental microwear patterns (Lucas, 1994). Thus, some of the observed patterns might be caused by phytoliths, other silica particles, or exogenous grit on food in addition to the food particles themselves. Clearly, more lab and field studies (e.g., Lucas, 1994; Lucas and Teaford, 1995;

Maas, 1991, 1994a; Strait, 1993; Strait and Overdorff, 1994, 1995; Teaford and Glander, 1991, in press; Ungar, 1992b, 1994; Ungar et al., 1995) are needed to sort through the relative effects of different abrasives in different environments. For instance, it might be that the size or shape of phytoliths and soil particles lead to characteristic microwear patterns which could ultimately be used in paleobiological interpretations (Ungar 1992b, 1994; Walker and Hagen, 1994). Another point to keep in mind is that this study focused on the molars of these species. Additional analyses of other teeth should tell us more about the method and frequency with which abrasives were ingested by these creatures. This would give us new insights into such topics as the degree of arboreality of the Fayum primates and the importance of incisal preparation in their feeding (e.g., Ungar, 1994; Ungar and Teaford, in press).

The second point we wish to emphasize is that, in this age of narrowly specialized techniques, collaborative work is the key to the future of paleobiology. Each paleobiological technique, be it bone isotope analysis, standard functional morphology, dental microstructure or microwear, etc., gives us but one piece of a complicated puzzle. Our task is to put that puzzle together as accurately as possible. To do so, we need the best information we can get from all available sources.

In this study, we have used two approaches to gain new insights into the paleobiology of the Fayum anthropoids. This is not to say that these are the best approaches or the only approaches to be used in this situation. We merely wish to note that if either had been used separately, we would have had a much weaker case to present. The combination of corroborative evidence from these approaches has also given us new insights into possible interpretations of each data set. We hope that this will encourage future collaborative work, which will in turn push paleobiological analyses closer to their potential.

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